Survival and mortality of grasshopper egg pods in semi-arid cereal cropping areas of northern Benin

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Abstract

Surveys of egg pods of agriculturally important grasshoppers were carried out in northern Benin between 1992 and 1995. Searches were made of oviposition sites under shrubs of the perennial legume *Piliostigma thonningi* along field margins. In 1993 and 1995, surveys were extended to include sorghum, *Sorghum bicolor*, and the perennial thatch grass *Vetiveria nigritana*. The four principal grasshopper species found at these oviposition sites were *Hieroglyphus daganensis* Krauss, *Cataloipus fuscocoeruleipes* Sjöstedt, *Kraussaria angulifera* (Krauss) and *Tylotropidius gracilipes* Brancsik comprising 86% of 4545 identified egg pods while 651 egg pods could not be identified to species level. Predation by meloid beetles (*Epicauta, Mylabris* and *Psalydolytta* spp.) varied between 0 and 50% for the four dominant grasshopper species. From 1993 and 1994 data, nymphal eclosion from egg pods damaged by meloids was significantly lower than emergence from undamaged egg pods. The hymenopterous parasitoids *Scelio africanus* Risbec and *S. mauriticanus* Risbec were reared from the four dominant grasshopper species and parasitism levels of 0.0–3.3% were recorded from these hosts. There were significant differences in nymphal emergences between parasitized and unparasitized egg pods of *H. daganensis*.

Introduction

Orthoptera generally oviposit in the upper soil layers producing egg masses which may or may not be enclosed by a protective wall. In the latter case, secretions from female accessory glands adhere to soil particles forming a capsule of cemented soil around the oothecae or egg cases (Uvarov, 1977; Greathead, 1992). Secretions may also form a foam plug between the soil surface and oothecae providing a possible route for emerging nymphs to follow to the soil surface during eclosion (Ewer, 1977).

Egg pods are found at different times during the life cycle of a particular grasshopper or locust species (Chapman, 1961; Fishpool & Popov, 1984; Mestre, 1988). In tropical regions with a marked rainy or monsoon season, species with adult diapause oviposit during the early part of the monsoon season and survive the dry season as immature adults, while those with egg diapause oviposit at the end of the monsoon season and overwinter in the egg stage. Continually reproducing species survive the dry season as adults but can undergo small-scale breeding if habitat conditions become favourable. Most economically important grasshopper species in Africa are univoltine and have an egg diapause stage.

Greathead (1963) provided an extensive catalogue of the natural enemies affecting embryonic and post-embryonic

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orthopteran stages. In the Afrotropical region, 19 species of egg parasitoids were recorded of which 17 were *Scelio* spp. (Hymenoptera: Scelionidae). From the 83 species of egg predators, 23 were beeflies (Diptera: Bombyliidae) and 14 were blister beetles (Coleoptera: Meloidae). The oothecal stage is considered to be especially vulnerable to attack by natural enemies since egg pods remain in the soil for one to seven months.

The present work forms part of a larger study being undertaken in northern Benin which involves evaluating the impact of natural enemies affecting grasshopper egg pods, determining if seasonal control measures are necessary by assessing egg pod densities and investigating whether mechanical destruction of egg pods during the dry season by farmers may cause long-term reductions in grasshopper numbers.

Between 1992 and 1995, surveys were carried out in northern Benin to: (i) identify possible oviposition sites of agriculturally important egg diapause grasshopper species; (ii) ascertain the effects of natural enemies on nymphal emergence; and (iii) to assess differences in natural enemy levels between seasons, grasshopper species and oviposition sites. Northern Benin is in a high rainfall zone (800–1000 mm) and the monsoon or rainy season occurs between April and October. Important rain-fed crops are sorghum, millet, maize, cotton, groundnuts and rice, while irrigated tomatoes, onions and potatoes are grown during the early part of the dry season.

Materials and methods

Field collection of egg pods

Surveys were based in the districts of Malanville (11°40'N, 30°30'E), Karimama (12°03'N, 3°11'E) and Madekali (11°41'N, 3°33'E). All three districts lie on the southern shores of the Niger and Sadoré Rivers. Surveys were carried out between May and June each year and were timed to coincide with the start of the monsoon season, so the clay-textured soils were sufficiently moistened to allow egg pods to be lifted with mechanical implements but before widespread nymphal hatching had taken place. Since egg pods were laid at the end of the previous monsoon season, surveys in 1992–95 reflected oviposition activities in 1991–94 respectively.

Several egg diapause grasshopper species were known to oviposit preferentially under shrubs or trees (Popov *et al.*, 1990), so searches for egg pods were primarily carried out under shrubs of the legume *Piliostigma* (=*Bauhinia*) *thonningi*. This plant was chosen because it was an easily recognizable perennial, forming extensive stands of 1–5 m in height at the margins of cultivations or occurring in small groups within cultivated areas. *Piliostigma* is found in secondary forests throughout the subhumid zones of Africa with more than 700 mm annual precipitation (von Maydell, 1990).

Before searches could be started, the lower branches of each shrub were excavated using machetes and the soil litter was cleared with rakes. The soil was then carefully scraped away with short-handled hoes to expose any egg pods which may have been present at a depth of 20–120 mm. Egg pods were lifted using trowels or pen knives and placed in labelled plastic containers before transportation to the field laboratory at Malanville. The soil under each shrub was searched in a radial manner and searches usually extended to 1–3 m away from the main trunk. Five to twenty *Piliostigma* shrubs were searched in four study sites in each of the three districts for every year of the survey work.

In 1993 and 1995, clumps of the perennial grass *Vetiveria nigritana* were investigated as possible oviposition sites initially because of suggestions made by farmers assisting in surveys. The height of desiccated *Vetiveria* clumps varied from 0.2–0.5 m during the dry season and between 1.0–2.5 m in the monsoon season. Radial searches extended to between 0.3–0.8 m from the centre of each clump. *Vetiveria* is present throughout west Africa especially in the flood plains of the Niger delta (Anon., 1993). In northern Benin, its leaves are used to make traditional thatching and enclosures. As further comparisons in 1993 and 1995, searches were also made in fields of sorghum, *Sorghum bicolor*, harvested during the previous rainy season, with egg pod samples being taken in visualized 1 m^2 quadrats centred around desiccated stalks. At each study site, 15–30 *Vetiveria* and *Sorghum* samples were taken.

For *Piliostigma* and *Vetiveria*, the radius of search (r) was measured using a 30 m tape and egg pod densities were calculated from the circular areas searched. Generally, study sites contained a mixture of the three oviposition sites and covered 1–5 ha in area.

Rainfall data for Malanville was provided by the Centre d'Action Regionale pour le Developpment Rural (CARDER) for Borgou Province.

Laboratory incubations

Preliminary species identifications of collected egg pods were made using descriptions given by Chapman (1961), Chapman & Robertson (1958) and Popov *et al.* (1990). Egg pods were categorized as either being viable (nymphal eclosion from undamaged and unattacked egg pods), non-viable (failure to hatch due to inherent inviability and/or mechanical damage to egg pods during excavation), decayed (oviposited in excessively damp soil), dehydrated (oviposited in excessively dry soil or subjected to excessive desiccation during the dry season), predated (by meloids or other predators) or parasitized by *Scelio* spp. Meloid predation was confirmed by the presence of larvae or pupae within egg pods or by characteristic holes in egg pod walls signifying attack (Popov *et al.*, 1990).

In 1992, egg pods were incubated in plastic boxes with moistened tissue paper to ascertain the identity of each grasshopper species. This was later discontinued and egg pods collected from 1993 onwards were incubated individually in glass tubes covered with muslin gauze and containing moistened sandy soil. Egg pods were checked every one or two days for the emergence of grasshopper nymphs, predators and/or parasitoids. Emerged nymphs were counted and transferred to large ventilated wooden cages while natural enemies were killed and placed in an insect collection for later taxonomic identification.

Data analysis

Summary tables were constructed detailing the percentages of viable and non-viable egg pods as well as egg pods classed as decayed, dehydrated or from which natural enemies were identified.

For the dominant grasshopper species, differences in eclosion success between undamaged, predated and parasitized egg pods were assessed using regression analysis specifying Poisson errors under the Generalized Linear Models procedure (SAS Institute Inc., 1990). Eclosion data were transformed using $\log_{10}(x+1)$, where x = numbers of nymphs emerging over a 30 day incubation period. To determine if the percentages of eggs parasitized per egg pod differed between parasitoid species or for host species, one-way analyses of variance (ANOVAs) were conducted. Percentage data were arc sine transformed prior to analysis.

Mixed model nested factorial ANOVAs (SAS Institute Inc., 1990) were performed for: (i) data obtained from *Piliostigma* between 1992–1995 to determine if there were any differences in meloid predation, scelionid parasitism or egg pod density between the dominant grasshopper species or survey years; and (ii) data obtained from *Piliostigma*, *Vetiveria* and *Sorghum* in 1993 and 1995 to detect any differences in meloid predation, scelionid parasitism or egg pod density between the three oviposition sites or dominant grasshopper species. Replication was provided by data from four survey sites studied in each of three districts for each of the survey years. Relevant higher order interactions were specified in all cases. Data for meloid predation were transformed using arc sine (range 0–100%) and a squareroot $(x+0.5)$ transformation was used for percentage parasitism (range 0–30%) following guidelines given by Gomez & Gomez (1984), while egg pod densities were transformed using $\log_{10}(x+1)$ to normalize error variances.

Results

Rainfall in the Malanville area has an unimodal pattern with the peak generally in August or September. Surveys were conducted in late May or early June after c. 150–200 mm had been recorded.

A total of 4545 egg pods was collected from the three oviposition sites in four years, 86% of egg pods were identified to species or subfamily level while 14% remained unidentified (table 1). Ten grasshopper species were recorded from incubations, but the four most commonly encountered species were *Hieroglyphus daganensis* Krauss, *Cataloipus fuscocoeruleipes* Sjöstedt, *Kraussaria angulifera* (Krauss) and *Tylotropidius gracilipes* Brancsik (Orthoptera: Acrididae) which comprised 58%, 18%, 13% and 3.9% respectively of all identified egg pods. Of the 651 unidentified egg pods, 37% and 40% were from the 1992 and 1995 surveys respectively. In 1992, egg pods were incubated on damp tissue paper rather than in moistened sand and many could not be identified because the rapid growth of saprophytic fungi prevented nymphal eclosion. Field collections in 1995 were much lower than previous years and a large number of egg pods could not be identified because they failed to hatch during incubation. During the 1995 survey, 51% of *H. daganensis* egg pods were classed as dehydrated and 58% of *C. fuscocoeruleipes* were rotten (table 1).

Egg pods of *C. fuscocoeruleipes* were easily damaged during excavation. For example, in 1993 a total of 153 egg pods were collected but only 28 (18%) could be categorized as truly undamaged specimens without any signs of rupture to foam plugs or egg pod walls and where at least one nymph emerged.

Predation

Scarabeid and tenebrionid larvae were present in soil litter but were not thought to be specific predators of egg pods and none were found within egg pods. Bombyliid larvae were not found to cause high levels of predation and three adults emerged from 19 larvae incubated between 1992 and 1995 (table 2). One bombyliid larva was found near unidentified egg pods in 1995 but the adult failed to emerge.

A total of 307 late instar meloid larvae and pupae were collected mostly from within egg pods but only ten individuals belonging to eight species emerged (table 2). The highest numbers were collected in 1994 when 210 larvae or pupae were found while 12 were collected in 1992, 85 in 1993 and none in 1995. Infection of meloid larvae by an entomopathogen was suspected in 1992 and 1993 because several were found which were extremely desiccated or mummified with a pink body colour. The discovery of a single larva in 1993 with these symptoms and also bearing synemmata was confirmed as being caused by the fungus *Cordyceps* sp. (H.C. Evans, personal communication). Percentage infection of meloids by *Cordyceps* sp. was estimated at 1.2% and 31% in 1993 and 1994 respectively. Four unidentified scarabeid larvae were also found infected by *Cordyceps* sp. in 1994.

Parasitism

Parasitoids were obtained from 66 egg pods of *H. daganensis*, *C. fuscocoeruleipes*, *K. angulifera*, *T. gracilipes* and *Zacompsa festa* Uvarov (Orthoptera: Acrididae). *Scelio africanus* Risbec (Hymenoptera: Scelionidae) was found in 20 egg pods, *S. mauritanicus* Risbec in 41 egg pods and *Scelio* sp. (possibly *S. pulchripennis* Brues) in five egg pods from all five host species. *Scelio africanus* and *S. mauritanicus* were not considered to be host specific but *Scelio* sp. was only reared from *Z. festa* in 1994. No parasitoids were recorded from surveys performed in 1995.

Scelio spp. parasitized a relatively small number of eggs within grasshopper egg pods. Excluding the 1992 data, where different incubation procedures were used, *S. mauritanicus* parasitized 14% eggs per egg pod (n = 36 egg pods, range = 1.7–51%, all grasshopper species), *S. africanus* parasitized 15% of eggs (n = 13, range = 1.4–72%) but *Scelio* sp. parasitized 57% eggs (n = 5, range = 5.9–100%). This was significantly greater than *S. mauritanicus* or *S. africanus* ($F_{2,48} = 5.08$, $P < 0.01$). In 1994, sex ratios of parasitoids emerging from parasitized egg pods of *H. daganensis* were recorded. A male:female ratio of 1.0:2.1 was estimated for *S. mauritanicus* from 28 egg pods and 137 parasitoids, while a ratio of 1.0:3.0 was found for *S. africanus* from two egg pods and eight individuals (G. Goergen, personal communication).

Effects of natural enemies on nymphal eclosion

Only eclosion data obtained in 1993 and 1994 were used since unsuitable incubation procedures were employed in 1992 and just two undamaged egg pods were found during the 1995 survey. The lowest numbers of nymphs emerging from undamaged or unattacked egg pods were recorded from *T. gracilipes* (table 3).

Predation significantly reduced nymphal eclosion for all of the four dominant grasshopper species. For parasitism,

Table 1. Viability and mortality of grasshopper egg pods collected from the legume *Piliostigma thonningi*, the perennial *Vetiveria nigritana* and from *Sorghum bicolor*, 1992–1995.

Oviposition site and year	n	Percent of egg pods in each category				
		Attack by non-meloid predators	Decayed	Dehydrated	Non-viable	Viable
Piliostigma						
1992						
Cataloipus fuscocoeruleipes	197	3.1	1.5	2.5	0	74
Hieroglyphus daganensis	136	3.0	0.7	12	0	77
Kraussaria angulifera	22	9.1	4.6	9.1	0	55
Pyrgomorpha cognata species complex	1	0	0	0	0	100
Tylotropidius gracilipes	83	3.6	0	0	0	93
Catantopinae	5	0	0	0	0	80
unidentified	238	15	29	7.6	23	0
Total	682					
1993						
C. fuscocoeruleipes	232	11	8.6	1.7	3.0	26
H. daganensis	544	7.7	6.6	2.2	2.0	57
Homoxyrrhepes punctipennis (Walker)	1	0	0	0	0	100
K. angulifera	100	0	6.0	0	2.0	75
P. cognata	1	0	0	0	0	0
T. gracilipes	11	0	0	0	9.1	73
Zacompsca festa	1	0	0	0	0	100
unidentified	85	4.7	20	5.9	44	0
Total	975					
1994						
Acorypha glaucopsis (Walker)	1	0	0	0	0	100
C. fuscocoeruleipes	203	5.9	1.0	0.5	0	48
Hieroglyphus daganensis	1251	3.4	5.8	4.7	0.1	57
Homoxyrrhepes punctipennis	3	0	0	0	0	100
K. angulifera	316	0	7.3	1.6	0.3	62
Orthochtha venosa (Ramme)	5	0	0	0	0	100
P. cognata	3	0	0	0	0	100
T. gracilipes	42	0	2.4	0	0	76
Z. festa	239	6.3	0.4	0.4	0.4	90
Catantopinae	3	0	0	0	0	100
unidentified	60	42	6.7	6.7	43	0
Total	2126					
1995						
C. fuscocoeruleipes	19	0	58	11	26	0
Hieroglyphus daganensis	89	0	25	51	7.8	2.3
K. angulifera	21	0	0	71	4.8	0
T. gracilipes	2	0	0	0	100	0
unidentified	248	0.4	7.7	85	2.0	0
Total	379					
Vetiveria						
1993						
C. fuscocoeruleipes	83	21	0	1.2	2.4	8.4
H. daganensis	202	9.4	1.5	1.5	2.5	56
Oedaleus nigeriensis Uvarov	1	0	0	0	0	100
unidentified	6	17	17	0	67	0
Total	292					
1995						
C. fuscocoeruleipes	3	0	33	33	33	0
H. daganensis	8	0	50	38	0	0
unidentified	5	0	20	40	40	0
Total	16					
Sorghum						
1993						
C. fuscocoeruleipes	26	27	3.9	0	0	7.7
H. daganensis	32	19	0	0	0	47
K. angulifera	1	0	0	0	0	100
unidentified	2	100	0	0	0	0
Total	61					
1995						
C. fuscocoeruleipes	1	0	0	0	100	0
H. daganensis	4	0	25	0	0	0
K. angulifera	2	0	0	0	0	0
unidentified	7	0	0	29	57	0
Total	14					

Table 2. List of natural enemies from grasshopper egg pods collected in northern Benin.

Natural enemy	Grasshopper host	Year(s) collected
Hymenoptera: Scelionidae		
Scelio africanus	*Cataloipus fuscocoeruleipes*	1992, 1993
	Hieroglyphus daganensis	1992, 1993, 1994
	Kraussaria angulifera	1992, 1994
	Tylotropidius gracilipes	1994
S. mauritanicus	*C. fuscocoeruleipes*	1992, 1994
	H. daganensis	1993, 1994
	K. angulifera	1994
	T. gracilipes	1992
Scelio sp. (*S. pulchripennis* Brues?)	*Zacompsa festa*	1994
Scelio sp.	Catantopinae	1992
Diptera: Bombyliidae		
Systoechus littoralis	*C. fuscocoeruleipes*	1992
	nr. *H. daganensis* and *Z. festa*	1994
S. segetus	nr. *H. daganensis*	1992
Coleoptera: Meloidae		
Epicauta sp.	*K. angulifera*	1994
Mylabris haemorrhoa King	nr. egg pods	1993
M. sp. nr. *bifasciata* De Geer	*C. fuscocoeruleipes*	1993
M. sp. nr. *holosericia* King	*C. fuscocoeruleipes*	1994
	H. daganensis	1994
Mylabris sp.	*H. daganensis*	1994
Psalydolytta fusca Olivier	*C. fuscocoeruleipes*	1993
P. remedelli Borchmann	*C. fuscocoeruleipes*	1993
	H. daganensis	1993
P. vesta Dufour	*C. fuscocoeruleipes*	1993
Ascomycotina: Pyrenomycetes		
Cordyceps sp.	meloid larvae	1993, 1994

significant differences in eclosion occurred only for *H. daganensis* (table 4).

Comparison of grasshopper species recovered from Piliostigma *1992–1995*

Egg pod density was significantly higher in 1994 for *H. daganensis, C. fuscocoeruleipes, K. angulifera* and *T. gracilipes* and lowest in 1995 ($F_{3,132} = 7.13$, $P < 0.01$) (fig. 1). Densities of *H. daganensis* were significantly greater compared to the other three grasshopper species ($F_{3,132} = 33.20$, $P < 0.0001$). The highest levels of meloid predation were recorded in 1994 ($F_{3,132} = 13.88$, $P < 0.0001$) and predation was significantly greater for *C. fuscocoeruleipes* ($F_{3,132} = 13.93$, $P < 0.0001$). Scelionid parasitism was highest in 1992 and lowest in 1995 ($F_{3,132} = 3.11$, $P < 0.05$). Parasitism was significantly higher for *H. daganensis* and *C. fuscocoeruleipes* compared to *K. angulifera* and *T. gracilipes* ($F_{3,132} = 2.74$, $P < 0.05$) (fig. 1).

Comparison of oviposition sites in 1993 and 1995

Hieroglyphus daganensis and *C. fuscocoeruleipes* were the two grasshopper species analysed because only two egg pods of *K. angulifera* and none of *T. gracilipes* were found from *Vetiveria* or *Sorghum* during the period when comparative surveys were performed.

The lowest egg pod densities were recorded from *Sorghum* ($F_{2,92} = 13.12$, $P < 0.001$) but there were no differences in meloid predation ($F_{2,92} = 1.56$, $P > 0.05$) or parasitism ($F_{2,92} = 2.37$, $P > 0.05$) between the three oviposition sites despite parasitism not being recorded from *Sorghum*. Egg pod density, meloid predation and scelionid parasitism were all higher from collections performed in 1993 compared to 1995 ($F_{1,92} = 18.59$, $P < 0.01$; $F_{1,92} = 26.34$, $P < 0.001$; and $F_{1,92} = 11.15$, $P < 0.01$ respectively) (fig. 2).

Discussion

Prior to these surveys, it had not been reported whether *H. daganensis, C. fuscocoeruleipes* or *T. gracilipes* oviposited under *Piliostigma* shrubs or *Vetiveria* grass clumps in west Africa. The initial aim was to study egg pods of *K. angulifera* which was known to strongly prefer many species of shrubs and trees for oviposition (Bindra & Amatobi, 1981; COPR, 1982).

Other orthopteran species also have specific oviposition requirements. *Oedaleus senegalensis* (Krauss) (Orthoptera: Acrididae) is an important cereal pest in west Africa, preferring to lay egg pods in uncultivated areas but in cultivated fields females will oviposit in plough ridges rather than furrows (Amatobi, 1985; Popov, 1980). In South Africa, egg laying by the African migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire) (Orthoptera: Acrididae), was mainly concentrated along crop interrows in maize and within clearings in wheat crops (Price, 1991).

Aggregation of egg pods between shrubs of *Piliostigma* or clumps of *Vetiveria* was observed but not quantified statistically. For example, in 1994, 231 egg pods were collected from under a single *Piliostigma* shrub while only 12–20 egg pods were found under shrubs within a 20 m radius. This aggregation was likely to have resulted from oviposition by females in areas with optimal microclimatic features of soil moisture and compaction, the possible use of oviposition pheromones, as well as the effects of non-reproductive behaviour including social aggregation (Clark, 1948;

Table 3. Nymphal numbers recorded from undamaged grasshopper egg pods and egg pods attacked by meloid predators or scelionid parasitoids.

Species	Year	Egg pods						
		Undamaged[a]			Meloid predation		Scelionid parasitism	
		n	No. nymphs pod^{-1}	Emergence period (days)	n	No. nymphs pod^{-1}	n	No. nymphs pod^{-1}
Hieroglyphus daganensis	1993	185	53 (1.6)	6.5 (0.6)	130	16 (2.3)	9	51 (10)
	1994	338	42 (1.0)	9.6 (0.7)	337	16 (1.3)	30	30 (3.0)
	1995	2	12 (1.5)	1.0 (0)	15	5.3 (3.0)	0	–
Cataloipus fuscocoeruleipes	1993	28	76 (6.6)	17 (2.5)	110	4.2 (1.5)	6	54 (12.7)
	1994	14	52 (8.5)	8.6 (3.8)	111	3.6 (1.2)	1	12 (–)
	1995	0	–	–	1	0.0 (–)	0	–
Kraussaria angulifera	1993	62	66 (3.2)	9.5 (1.0)	17	50 (1.5)	0	–
	1994	50	67 (4.0)	14 (1.9)	93	20 (2.5)	2	53 (4.5)
	1995	0	–	–	7	1.7 (1.9)	0	–
Tylotropidius gracilipes	1993	6	24 (4.8)	1.0 (–)	3	24 (1.7)	0	–
	1994	19	27 (2.8)	4.3 (1.2)	7	15 (4.7)	1	5.0 (–)
	1995	0	–	–	0	–	0	–

Standard errors of means in parentheses; [a]excluding egg pods injured during excavation.

Popov, 1959; Price, 1991). Clumping within rather than between oviposition sites has been noted by Fisher (1992) in southwest Montana. Higher numbers of egg pods of *Aulocara elliotti* (Thomas) (Orthoptera: Acrididae) were found on the southern sides of clumps of crested wheatgrass which also had the warmest soil temperatures.

Egg pods of *C. fuscocoeruleipes* were easily broken during excavation from the soil because they were relatively long and slender (60–100 mm length, 7–10 mm radius) compared to *H. daganensis* (30–50 mm length, 7–12 mm radius), *K. angulifera* (50–80 mm length, 10–13 mm radius) or *T. gracilipes* (35–50 mm length, 5–8 mm radius). Additionally, egg pods

Table 4. Summarized results of Poisson regression of the influence of attack by predators or parasitoids on nymphal eclosion.

Species	Source	Predation		Parasitism	
		χ^2	Parameter estimate	χ^2	Parameter estimate
Hieroglyphus daganensis	Intercept		2.8 (0.1)		3.4 (0.1)
	Year	0.8	–0.4 (0.1)	19***	0.5 (0.2)
	Attack	317***	1.0 (0.1)	3.9*	0.3 (0.1)
	Year*Attack	19***	0.6 (0.1)	2.6	0.2 (0.2)
Cataloipus fuscocoeruleipes	Intercept		1.3 (0.4)		2.5 (1.2)
	Year	0.0	–0.3 (0.5)	2.6	1.6 (1.2)
	Attack	116***	2.7 (0.4)	2.0	1.5 (1.2)
	Year*Attack	1.6	0.7 (0.6)	1.0	–1.2 (1.2)
Kraussaria angulifera	Intercept		3.0 (0.1)		4.0 (0.3)
	Year	23***	1.0 (0.2)	0.1	0.0 (0.1)
	Attack	48***	1.2 (0.1)	0.6	0.2 (0.3)
	Year*Attack	25***	–1.0 (0.2)	–	–
Tylotropidius gracilipes	Intercept		2.8 (0.3)		1.6 (1.1)
	Year	0.5	–0.3 (0.5)	0.3	–0.1 (0.2)
	Attack	4.4*	0.5 (0.4)	2.6	1.7 (1.1)
	Year*Attack	0.1	0.2 (0.5)	–	–

χ^2 values only given for sources of variation and not for intercepts or other parameter estimates; *$P < 0.05$; ***$P < 0.001$; df for sources of variation = 1; Standard errors for parameter estimates in parentheses.

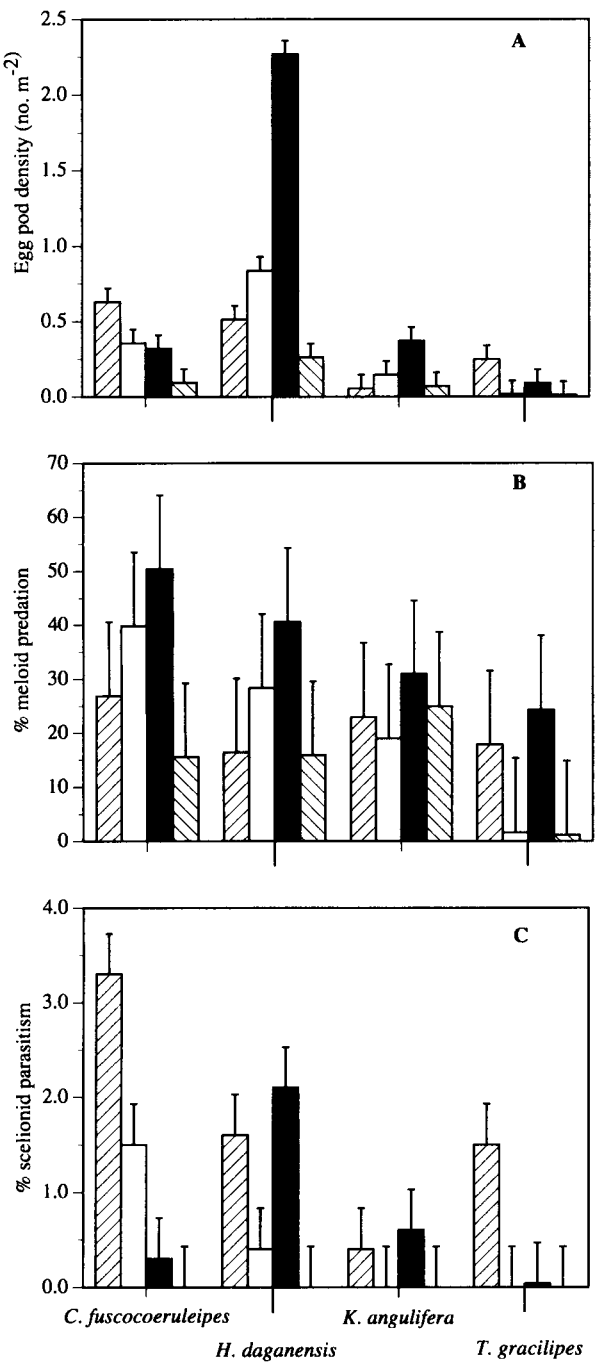

Fig. 1. Mean values of egg pod density (A), meloid predation (B) and scelionid parasitism (C) for the four dominant grasshopper species found under *Piliostigma* in 1992 (▨), 1993 (□), 1994 (■) and 1995 (▧).

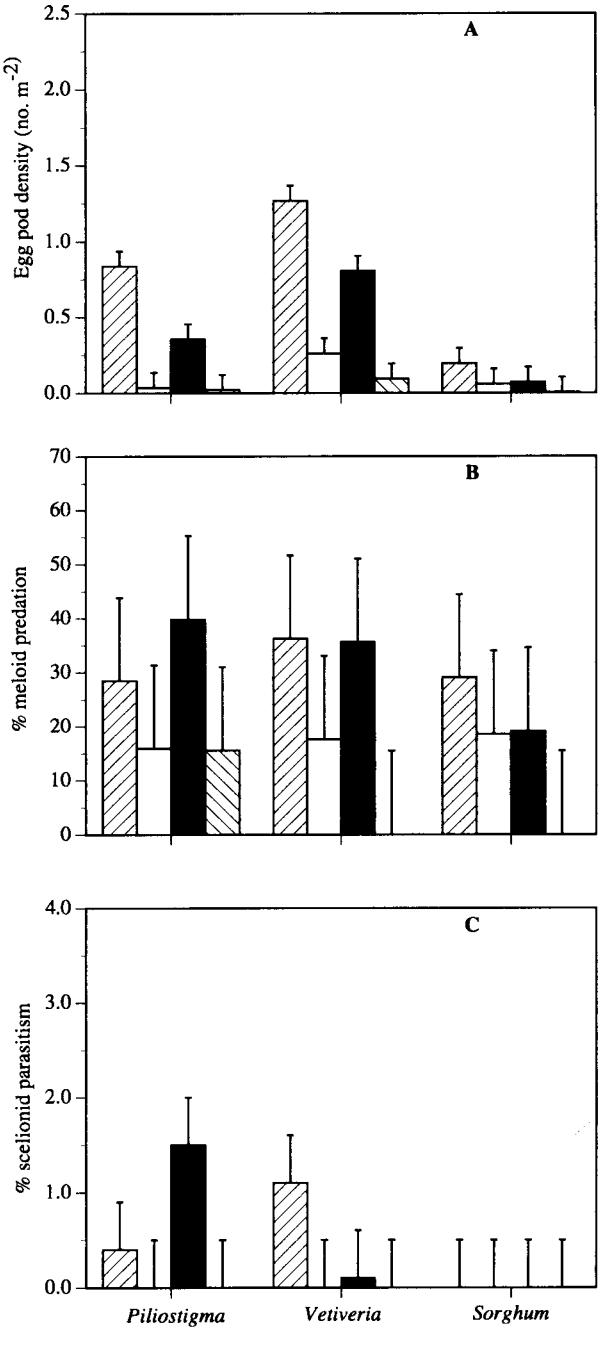

Fig. 2. Comparisons of egg pod density (A), meloid predation (B) and scelionid parasitism (C) between the three oviposition sites for *Hieroglyphus daganensis* in 1993 (▨) and 1995 (□) and for *Cataloipus fuscocoeruleipes* in 1993 (■) and 1995 (▧).

of *H. daganensis* and *K. angulifera* formed very hard capsules which were extremely resistant to mechanical penetration.

Meloid predation may have been higher for *C. fusco-coeruleipes* because egg pods were longer and less resistant to mechanical penetration facilitating the location and entry of oothecae by predatory larvae. Eclosion from undamaged egg pods of either *H. daganensis, C. fuscocoeruleipes, K. angulifera* or *T. gracilipes* was significantly greater than from egg pods attacked by meloids. This implies that viability is reduced even when egg pods do not contain any meloid larvae but show signs of meloid attack signified by the presence of one or more pits through the egg pod walls. In northwest Mali,

Psalydolytta pilipes Maklin and *P. vestita* Dufour (Coleoptera: Meloidae) were reared from egg pods of several grasshopper species. The only exception was *O. senegalensis* whose smaller, more slender egg pods may have restricted larval development (Grunshaw *et al.*, 1994). *Psalydolytta fusca* Olivier (Coleoptera: Meloidae) has been reared from *C. fuscocoeruleipes* egg pods in Gambia (Selander & Laurense, 1987).

The present report of *Cordyceps* sp. from meloid larvae was interesting as the fungal genus is most common in humid, tropical forests (Samson *et al.*, 1988) but scarce in areas of depleted forests and agricultural land which characterized our surveys.

All *Systoechus* spp. are predators of grasshopper and locust egg pods (Greathead, 1958). *Systoechus littoralis* Bowden and *S. segetus* Bowden (Diptera: Bombyliidae) have previously been identified from Ghana (D.J. Greathead, personal communication).

Rearings of *S. africanus* and *S. mauriticanus* from *H. daganensis, C. fuscocoeruleipes, K. angulifera* and *T. gracilipes* appear to constitute new host recordings based on previous literature (Nixon, 1958; Popov *et al.*, 1990; Siddiqui *et al.*, 1986). *Scelio* spp. in northern Benin are likely to be univoltine since their grasshopper hosts have one generation per year. Voltinism in *Scelio* has been found to alter with changes in latitude and host biology (Baker *et al.*, 1985). Parasitism by Scelio spp. involves the use of an anatomically and mechanically unique telescopic ovipositor system into the upper portions of orthopteran egg pods (Field & Austin, 1994). Popov (1959) argued that puparia discarded by adults of *S. sudanensis* Ferriere from parasitized eggs of *L. m. migratorioides* caused blockages preventing first instar nymphs from exiting egg pods. Evidence from the present study indicates that parasitism by *Scelio* spp. significantly reduced the numbers of nymphs emerging from egg pods of *H. daganensis*, where a larger sample size was available for comparison with unparasitized egg pods. For all grasshopper species, relatively small numbers of eggs were parasitized within individual egg pods.

The low levels of egg pod and egg parasitism recorded in the present study suggest that *Scelio* spp. do not have a major role in regulating grasshopper numbers. Meloid predators appear to be the dominant obligate arthropod natural enemies of egg pods and may cause some regulation in grasshopper numbers but these predators are also attacked by a fungal entomopathogen so limiting their effectiveness.

Laboratory incubations of grasshopper adults and nymphs collected from two sites in Malanville between 1992 and 1995 indicated regular low level infections of less than 4.0% caused by the fungal entomopathogen *Metarhizium flavoviride* but endoparasitoids were recorded only once during the four year study (Shah *et al.*, 1994, 1998). Hence, natural enemies reared from laboratory incubated hosts appear to be most active against oothecal rather than post-embryonic stages of grasshoppers but no attempts have been made so far to quantify losses due to predation of grasshopper nymphs or adults in northern Benin.

Abiotic factors have an important role in affecting the survival of orthopteran egg pods. For example, soil temperatures and rainfall have been shown to influence oothecal viability of *O. senegalensis* in Mali (Colvin, 1997). In the current study, very low numbers of egg pods collected in 1995 may have resulted from widespread flooding of oviposition sites during the previous season. Further investigations are required to determine the relationship between egg pod survival and abiotic conditions in northern Benin. A control strategy could then be developed combining biotic and abiotic factors to predict when mechanical destruction of egg pods by farmers should be undertaken to prevent crop damage.

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References

Amatobi, C.I. (1985) Oviposition preference and the influence of cultivation on egg hatching in *Oedaleus senegalensis* (Orthoptera: Acrididae). *Samaru Journal of Agricultural Research* **3**, 81–85.

Anon. (1993) *Vetiver grass: a thin green line against erosion*. 171 pp. National Research Council, Washington DC, National Academy Press.

Baker, G.L., Pigott, R. & Galloway, I. (1985) The phenology of *Scelio* spp. (Hymenoptera: Scelionidae), parasites of acridid eggs (Orthoptera: Acrididae) in south east Australia. pp. 268–275 *in* Chapman, R.B. (*Ed.*) *Proceedings of the 4th Australasian Conference on Grassland Invertebrate Ecology, Lincoln College, University College of Agriculture, Canterbury, New Zealand*. Caxton Press, Christchurch, New Zealand.

Bindra, O.S. & Amatobi, C.I. (1981) Bionomics of *Kraussaria angulifera* Krauss (Orthoptera: Acrididae) in northern Nigeria. *Samaru Journal of Agricultural Research* **1**, 59–67.

Chapman, R.F. (1961) Egg pods from grasshoppers collected in southern Ghana. *Journal of the Entomological Society of South Africa* **24**, 259–284.

Chapman, R.F. & Robertson, I.A.D. (1958) The egg pods of some tropical African grasshoppers. *Journal of the Entomological Society of South Africa* **21**, 85–112.

Clark, E.J. (1948) The ecology of British grasshoppers. *Transactions of the Royal Entomological Society of London* **99**, 173–222.

Colvin, J. (1997) Biotic and abiotic factors affecting the population dynamics of the Senegalese grasshopper, *Oedaleus senegalensis*. pp. 63–67 *in* Krall, S., Peveling, R. & Ba Diallo, D. (*Eds*) *New strategies in locust control*. Basel, Birkhaüser Verlag.

COPR (1982) *The locust and grasshopper agricultural manual*. 560 pp. London, Centre for Overseas Pest Research.

Ewer, D.W. (1977) Two functions of the foam plug of acridid egg pods. *Acrida* **6**, 1–18.

Field, S.A. & Austin, A.D. (1994) Anatomy and mechanics of the telescopic ovipositor system of *Scelio* Latreille (Hymenoptera: Scelionidae) and related genera. *International Journal of Insect Morphology and Embryology* **23**, 135–158.

Fisher, J.R. (1992) Location of egg pods of *Aulocara elliotti* (Orthoptera: Acrididae) in a field of crested wheat in Montana. *Journal of the Kansas Entomological Society* **65**, 416–420.

Fishpool, L.D.C. & Popov, G.B. (1984) The grasshopper faunas of the savannas of Mali, Niger, Benin and Togo. *Bulletin de l'Institute Fondamental d'Afrique Noire* **43**, 275–410.

Gomez, K.A. & Gomez, A.A. (1984) *Statistical procedures in agricultural research*. 2nd edn. 680 pp. New York, John Wiley and Sons.

Greathead, D.J. (1958) Observations on two species of *Systoechus* (Diptera: Bombyliidae) preying on the Desert Locust, *Schistocerca gregaria* (Forskål), in eastern Africa. *Entomophaga* **1**, 5–22.

Greathead, D.J. (1963) A review of the insect enemies of Acridoidea (Orthoptera). *Transactions of the Royal Entomological Society of London* **114**, 437–517.

Greathead, D.J. (1992) Natural enemies of tropical locusts and grasshoppers: their impact and potential as biological control agents. pp. 105–121 *in* Lomer, C.J. & Prior, C. (*Eds*) *Biological control of locusts and grasshoppers*. Wallingford, Oxon, CAB International.

Grunshaw, J.P., Mariko, S. & Troare, I. (1994) Field studies on the biology and economic importance of *Psalydolytta* spp. (Coleoptera: Meloidae: Meloinae) in Mali, West Africa. *Bulletin of Entomological Research* **84**, 493–502.

Mestre, J. (1988) *Les acridiens des formations herbeuses d'Afrique de l'Ouest*. 330 pp. Paris, Ministère de la Coopération et CIRAD/GERDAT.

Nixon, G.E.J. (1958) A synopsis of the African species of *Scelio* Latreille (Hymenoptera: Proctotrupoidea, Scelionidae). *Transactions of the Royal Entomological Society of London* **110**, 303–318.

Popov, G.B. (1959) Ecological studies on oviposition by *Locusta migratoria migratorioides* (R. & F.) in its outbreak area in the French Sudan. *Locusta* **6**, 5–63.

Popov, G.B. (1980) *Studies on oviposition, egg development and mortality in* Oedaleus senegalensis *(Krauss), (Orthoptera, Acridoidea) in the Sahel*. 48 pp. London, Miscellaneous Report No. 53, Centre for Overseas Pest Research.

Popov, G.B., Launois-Luong, M.H. & van der Weel, J.J. (1990) *Les ootheques des criquets du Sahel*. 153 pp. Niamey, Collection Acridologie Opérationnelle No. 7. Ministère des Affaires Étrangères des Pays-Bas et CIRAD/PRIFAS (France).

Price, R.E. (1991) Oviposition by the African migratory locust, *Locusta migratoria migratorioides*, in a crop environment in South Africa. *Entomologia Experimentalis et Applicata* **61**, 169–177.

SAS Institute Inc. (1990) *SAS/STAT® user's guide*, Version 6, 4th edn. Volume 1, 943 pp., SAS Institute Inc., Cary, North Carolina.

Samson, R.A., Evans, H.C. & Latgé, J.P. (1988) *Atlas of entomopathogenic fungi*. 187 pp. Berlin, Springer-Verlag.

Selander, R.B. & Laurense, A.A. (1987) On the immature stages of *Psalydolytta fusca* (Coleoptera: Meloidae). *Proceedings of the Entomological Society of Washington* **89**, 489–499.

Shah, P.A., Godonou, I., Gbongboui, C. & Lomer, C.J. (1994) Natural levels of fungal infections in grasshoppers in northern Benin. *Biocontrol Science and Technology* **4**, 331–341.

Shah, P.A., Gbongboui, C., Godonou, I., Hossou, A. & Lomer, C.J. (1998) Natural incidences of *Metarhizium flavoviride* infections from two grasshopper communities in northern Benin. *Biocontrol Science and Technology* **8**, in press.

Siddiqui, R.K., Irshad, M. & Mohyuddin, A.I. (1986) *Scelio* spp. as biocontrol agents of acridids. *Biocontrol News and Information* **7**, 69–76.

Uvarov, B.P. (1977) *Grasshoppers and locusts, a handbook of general acridology*. 481 pp. Volume 2. Cambridge University Press.

von Maydell, H.J. (1990) *Trees and shrubs of the Sahel: their characteristics and uses*. 525 pp. Weikersheim, Verlag Josef Margraf.

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